

Species Concepts in Pteridophytes: Summary and Synthesis

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Systematic pteridologists may be at a crossroads in their perception and treatment of species. Each of the papers in this symposium series presents a historical perspective, the state of the art, and a view to the future in considering what impact current research will have on the evolution of our theories, the direction of our research, and, ultimately, the development of our discipline. The first two papers (on primary divergence [Yatskievych and Moran, 1989] and reticulate evolution [Barrington et al., 1989]) cover the more familiar considerations of pteridophyte species. Both of these papers review how we have approached species in the past and explore how ongoing studies are modifying both the theoretical and the practical perception of species. Both contributions showed that to date species recognition has not been affected significantly by modern approaches. This may change, however, because fieldwork and examination of living specimens are now becoming standard components of revisionary studies. Thus far, molecular data have been used primarily to test hypotheses about the origin and interrelationships of species and have proven remarkably useful in evaluating polyploid complexes. The third contribution on cryptic species (Paris et al., 1989) explores the possibility that in some cases, traditional approaches may not yield an accurate picture of what constitutes natural evolutionary units. This paper raises the additional specter that these are not isolated cases and cryptic species may be much more common than currently recognized. The fourth contribution on agamosporous taxa (Gastony & Windham, 1989) presents convincing evidence that asexual species should be accorded greater status and consideration as dynamic evolutionary elements. Although typically regarded as entities without a future, agamosporous taxa can be genetically variable because of multiple origins and can add substantially to the taxonomic confusion of many groups by hybridizing with sexual congeners to produce new agamosporous species. The final paper on *Isoetes* species (Hickey et al., 1989) illustrates well that through the application of biosystematic approaches to the "fern allies," all of the predicted influences of cryptic species, ecological variants, and hybridization are conspiring to complicate modern species concepts in the microphyllous vascular cryptogams.

THE CHANGING VIEW OF SPECIES

In the papers constituting this symposium, several recurrent themes relating to the development of modern perceptions of species are evident.

1) Fieldwork has played an important role in providing a firmer foundation for assessing the limits of intraspecific variability. The collection of live plants has

been especially important in considering the primary divergence of species and the environmental component of morphological variability. Obviously, in modern revisions, fieldwork must continue to figure prominently.

2) Evidence from modern experimental approaches is having a great influence on changing our perception of the forces driving speciation, developing intraspecific variability, and maintaining isolation of species. Since 1950, the value of chromosomal information has been recognized, but more recently teaming chromosomal and isozymic data has proven to be a powerful approach for building new systematic hypotheses. Questions that cannot be answered by one technique are often resolvable by the other. It seems clear that revisions will need to incorporate evidence from at least one if not both of these techniques in developing a persuasive set of taxonomic guidelines. In addition, it is clear that chloroplast DNA analysis will be used with increasing frequency as an important data base for developing hypotheses concerning interspecific and intergeneric relationships.

3) Because it is evident that many of the morphological features that have figured prominently in defining species in the past are subject to parallel and convergent evolution and are heavily influenced by ecological conditions, we must continue looking for new characters and developing morphometric analyses of our accumulated data. The likely emergence of more and more cryptic species demands that we pay closer attention to less prominent characters in proposing species boundaries.

4) We must acknowledge the value of employing explicitly phylogenetic analyses in developing hypotheses of relationship. There are many programs and protocols (e.g., PAUP and PHYLIP) that are available for phylogenetic analysis of biochemical and morphological data sets. Revisions based exclusively on intuitive perceptions of evolutionary links between taxa can no longer be considered sufficient.

CONCEPTS AND DEFINITIONS

Three principal concepts emerge from the amalgamated contents of the papers in this symposium. Although the emphases given to these views of species are varied and the actual names applied may differ, I think that the fundamental ideas may be encapsulated by the following summary. The morphological species concept refers to groups whose boundaries are diagnosed by discontinuities in critical, qualitatively or quantitatively definable features of the available specimens. The biological species concept is applied to groups that do not necessarily differ morphologically but do have barriers to interbreeding. In nature, biological species may be difficult to recognize because they can be isolated solely by genetic differences, ecological tolerances, geological barriers, geographical distance, or by a combination of these features. The evolutionary species concept has been proposed to place a historical parameter on biological species and require definition of ancestral/descendent relationships. Even agamosporous species can be called good evolutionary species because they represent monophyletic clones of organisms. It seems, therefore, that the

different ideas about species depend on the amount and type of data available; as more data are available, more inclusive species concepts can be employed.

The crux of the matter is that our delimitation of a species should always represent a testable hypothesis. Ideally, there should be one concept that is the most robust, and that is applicable to both sexually and asexually reproducing species. We should attempt to delimit species that are consistent with this concept. Of those discussed above, the most widely applicable is the evolutionary species concept. To properly propose an evolutionary species, however, we should know 1) its morphological characteristics and how these differ from taxa that resemble it most clearly, 2) its breeding behavior and/or how it remains isolated from other species, 3) its ecological and geographical range, and 4) how it is related genealogically to its congeners. Clearly, this represents more than we know about most pteridophyte species and it is unreasonable to demand that all of this information be in hand before new species are proposed.

If we consider the evolutionary species *concept* as a goal of modern systematists, what should we call the steps or preliminary hypotheses along the way? Perhaps practical *definitions* can be employed as mileposts marking the route towards the evolutionary concept goal. These definitions can represent the best hypotheses that can be proposed based on the available data and the application of these definitional mileposts can recognize the progressive acquisition of new data. When morphological analyses of herbarium specimens are combined with geographical and ecological data (and at least this set of data should be considered basic in recognizing new taxa), the morphological definition is employed. Including data from natural or artificial crosses, chromosomes, isozymes, DNA, etc. leads to a more "biological" definition. By adding historical perspectives on the origins of taxa through paleobotanical and geological data as well as explicit arguments on character state evolution and ancestors, an evolutionary species can be proposed. I do not mean to imply that this is an endpoint—even the most seemingly robust evolutionary scenarios are still hypotheses open to further testing.

CONCLUSIONS AND PREDICTIONS

Several conclusions about pteridophyte species can be made from the information in this symposium. First, in pteridophytes, because there is not a good fossil record and extinction has erased much of the historical evidence for polarizing characters, it will continue to be difficult to propose evolutionary species at the diploid level. Second, Paris et al. (1989) have demonstrated that expanded data bases can modify our perception of species limits and can be used to develop strong biological species definitions even in the face of ambiguous morphological criteria. Certainly the demonstration that cryptic species may be prevalent in pteridophytes means that we must remain open minded regarding the sorts of applicable data. Ultrastructural and biochemical traits cannot be ignored simply because they are difficult to generate and observe directly. At the same time, we must evaluate critically what constitute significant characters in defining species. Third, in polyploid taxa (whether sexual or agamosporous),

chromosomal and isozymic data often allow us to make precise statements about the origin of lineages and so in many cases we may be able to apply a rigorous evolutionary species concept. Finally, it may be predicted that at all ploidy levels, the expanded application of chloroplast DNA data will be valuable in proposing and testing phylogenetic hypotheses.

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